Concerning the concept of extinct classes of Mollusca: or what may/may not be a class of mollusks

Ellis L. Yochelson

Research Associate, Department of Paleobiology, National Museum of Natural History, Washington, DC 20560-0121, U. S. A.

Abstract: In the notion of classes, all of whose members are extinct, at least two fundamental issues are intertwined: (1) what criteria should be used to assign a fossil to the Mollusca; and (2) what level of morphological distinctiveness is needed to establish a fossil as a representative of an extinct class. One may also ask how far the morphologic limits of extant classes should be extended. Several current textbooks recognize at least one class of extinct mollusks. There is no consistency in the number of extinct or extant classes in use, nor need there be while the field is still vigorously under discussion.

Key Words: classification, evolution, extinction, fossils, morphology

Class proposals for extinct mollusks, or fossils thought by some paleontologists to be mollusks, have been in the literature for about a century. Discovery of living examples of the Class Monoplacophora stirred both malacology and paleomalacology and the last four decades have seen new proposals of both extant and extinct classes. Study of specimens is far more informative than examination of photographs. Notwithstanding that point, sketches are included herein, but only for the purpose of making the text less obtuse. This essay repeats ideas written earlier (Yochelson, 1978, 1979) and, all my remarks should to be preceded with "in my view" or "in my opinion." Those fundamentally important phrases are eliminated, only to save space. Classification is a subjective activity and the higher one moves up in the Linnaean hierarchy, the greater the degree of subjectivity. "Authoritarianism is dangerous, especially for scientists, and the reader should approach my comments with a skeptical attitude" (Yochelson, 1979:324).

ISSUES

The more that has been learned of living animals, the more complex has become their classification. In 1758, Linnaeus did not use the category of phylum, but his equivalent has increased ten-fold. Over centuries, the relative importance assigned to various features by different workers has changed. For example, Molluscoidea was split off from Vermes and disappeared when Brachiopoda and Bryozoa came into use. The latter is now two phyla and some workers would also divide the former in two. The present concept of Mollusca is not necessarily sacrosanct. During one-quarter of a millennium, data on fossils have also dramatically increased and there is equally good reason to expect the number of higher-level taxa of extinct forms should also increase.

Defining a class as the taxon rank below a phylum is correct, though not particularly helpful. Much of acceptance or rejection in high-level systematics is based on the opinion of textbook authors. The fundamental question of whether extinct classes of mollusks are recognized is answered in the affirmative by reviewing paleontology texts of the last three decades. Consensus is that at least one extinct molluscan class, Rostroconchia (Pojeta *et al.*, 1972) is recognized in the Paleozoic; it features in a major paper (Waller, 1998). "One" is not large, but it constitutes a dramatic philosophical change from viewing Mollusca as containing only extant classes.

Which extinct class proposals are "reasonable" is another issue. The number of classes recognized among phyla varies widely. Within classes, the number of orders, families, or genera also varies widely. There are no rules to follow on the number and content of extinct and extant classes. How one decides whether a genus or a group of genera should be recognized as of class rank is yet a different issue.

A digression, which appears simplistic, is appropriate. The Class Gastropoda constitutes mollusks that have undergone torsion; all extant classes are based on features of soft anatomy. In the absence of torted soft parts, there are no fossils one can state with 100% confidence are Gastropoda. A paleontologist compares the shell of a living gastropod with a fossil shell; similarity of modern and fossil hard parts is at such a high level of probability, that the concept that it is a probability is forgotten. Classification is based on probability, not certainty.

For fossil mollusks to be considered an extinct class-rank taxon the hard part morphology should differ dramatically from that of other classes of Mollusca. To determine what features are dramatically different is as much a matter of art as it is of science. After defining species as a community of individuals "whose distinctive characters, are in the opinion of a competent specialist, sufficiently definite to entitle . . . a specific name" a fish specialist at the British Museum (Natural History), added "Groups of higher or lower rank . . . can be defined in the same way" (Regan, 1925:D1). In the game of classification, the only rule may be appeal to authority, a most unscientific approach. Cladistics and molecular systematics may appear more rigorous, but they too are ultimately grounded on certain assumptions; change the assumption and one changes the end result.

As a further complication in studying fossil mollusks that might have had more than one hard part, effects of taphonomy should not be ignored (Yochelson, 1984). Bizarre forms have been described, because modifications by sorting, transport, wear, and solution were ignored. Only after the taxon is satisfactorily defined by reference to the hard part(s) should one begin to speculate on soft parts and how they might have functioned. Listing interpretation of unknown anatomical features as the least significant criterion may not be popular, but it is the only way I see to understand molluscan fossils that do not closely resemble Recent mollusks. Three examples of possible extinct classes may help dispel some of this miasma. These are most familiar to me, but other proposals are equally worthy of discussion.

CLASS MATTHEVA

My proposal of this extinct class (Yochelson, 1966), which contained one genus, was based on the co-occurrence of two triangular-shaped, narrow pieces, each of which contained two deep cavities (Fig. 1). I was in error in suggesting the theoretical possibility of intermediate plates, for these were based on the presence of worn scraps. An assumption is that the cavities were for muscles and that two forms were anterior and posterior. I did not know which piece is anterior and which is posterior, and still do not know, but that uncertainly does not in any way affect

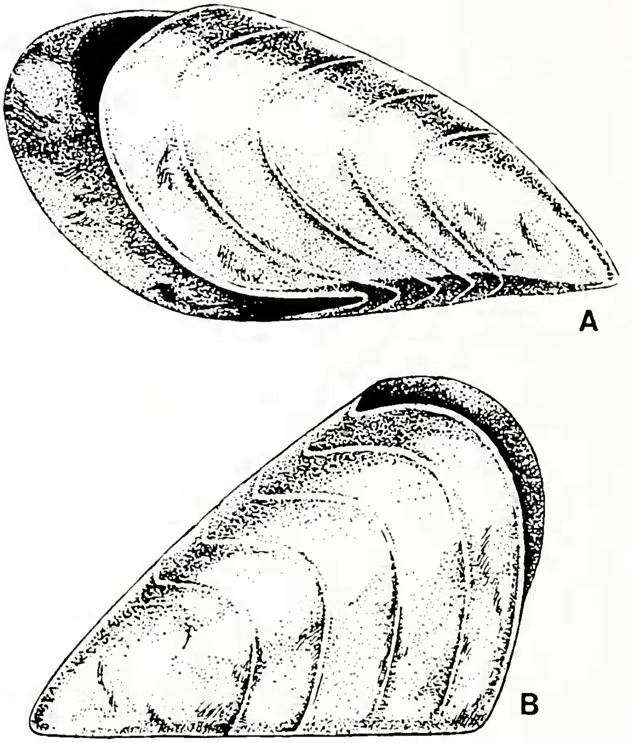

Fig. 1. Mattheva. **A.** One piece, possibly anterior. **B.** Another piece, possibly posterior. About three times natural size. (Yochelson, 1966, figs. 1 and 2).

the morphological uniqueness of this fossil. Specimens occur with algal domes. A paleoecological assumption is that the organisms did not cling to the substrate, but the weight of the two pieces helped maintain it in place during times the water was flowing.

Runnegar and Pojeta (1974) presented a reconstruction of the Late Cambrian *Matthevia*, and used a then undescribed intermediate (Runnegar *et al.*, 1979) to link it to an Early Ordovician polyplacophoran, *Chelodes*. That genus has only a single cavity and is broad and low, like the profile of a roof. I did not agree with their drawing, which resembled a seven-parted hedgehog (Yochelson 1978), nor did the latter suggestion of eight parts improve the reconstruction (Runnegar, 1983). There is evidence from fossils of only two thick heavy pieces, not the various slight modifications shown in their diagram. Runnegar *et al.* (1979) and Pojeta (1980) refuted my views, but it would be pedantry, to attempt to refute them here. Those not completely turned off by squabble should concordantly examine these papers.

One could expand the Polyplacophora to include *Matthevia*, strikingly different from all others, as is the approach in current literature. Alternatively, one could recognize a class that could have had more than one hard part, but whose parts do not resemble polyplacophoran plates of living taxa. My idea of a class has fallen on sterile ground, yet I remain mumpsimus. Because a paleontologist deals with hard parts, it is better to recognize smaller groups of more or less uniform "bauplan" than to have larger unwieldy groups. Gould (1989) used "shoehorn" for the process of cramming the wrong fossils into a taxon based on living material.

Polyplacophora have been reported from the Early Cambrian (Yu, 1984; 1990). If these fossils are part of the class – which I doubt – *Matthevia* is far off the main line of polyplacophoran evolution. If plates of *Preacanthochiton*, which most parties agree are polyplacophoran, are known from the earliest Early Ordovician, there is only a very short time to modify *Matthevia* from its bizarre shape to that approaching a modern chiton.

There are multiple possibilities in classification. A century and a quarter ago, von Ihering proposed that the Amphineura (= Polyplacophora of current literature) constituted a phylum. Most neomalacologists accept that polyplacophorans are quite different from most other mollusks and they are often put in a separate subphylum. Perhaps a phylum Amphineura, containing two classes, Polyplacophora and Mattheva would be appropriate. Of course, it does not follow that either von Ihering, Yochelson, or Runnegar *et al.* had the correct answer.

CLASS STENOTHECOIDA

My proposal for this class (Yochelson, 1968, 1969) was based on Early and Middle Cambrian bivalved fossils, commonly found as elongate, isolated valves; probably five or six genera fall within the class (Fig. 2). The valves are asymmetrical and inequivalved and have a single apical tooth and socket holding them together. Internally, one valve has many closely spaced ridges. Little can be mentioned about their paleoecology except that where they occur, they commonly are abundant. They are widespread in Asia (Yu, 1996) and North America.

As regards interpretation of *Stenothecoides*, "We offer the alternative suggestion that it may have been a bivalved monoplacophoran, with the lower (smaller?) valve formed by the sole of the foot" (Runnegar and Pojeta, 1974:316). This concept was repeated by Pojeta and Runnegar (1976:44), and seemingly there has been no further discussion.

Members of Class Bivalvia (= Pelecypoda of older literature) have two valves and if the choices were between that class or Monoplacophora, I would have preferred the former. There are inquivalve bivalves and asymmetric bivalves, but both are uncommon. The tooth and socket is quite unlike a hinge line. To place Stenothecoida within the Bivalvia would require such an expansion of the concept as to make it unpalatable. As an additional complication, a quarter of a century ago, the early Cambrian *Fordilla* (Pojeta *et al.*, 1973; Pojeta and Runnegar, 1974) was considered the ancestral member of Bivalvia. If that is true, then stenothecoids might be a dramatic morphologic expansion concurrently early in time with a conservative lineage. Adding this factor to the morphology, placing these aberrant fossils in an extinct class seemed reasonable.

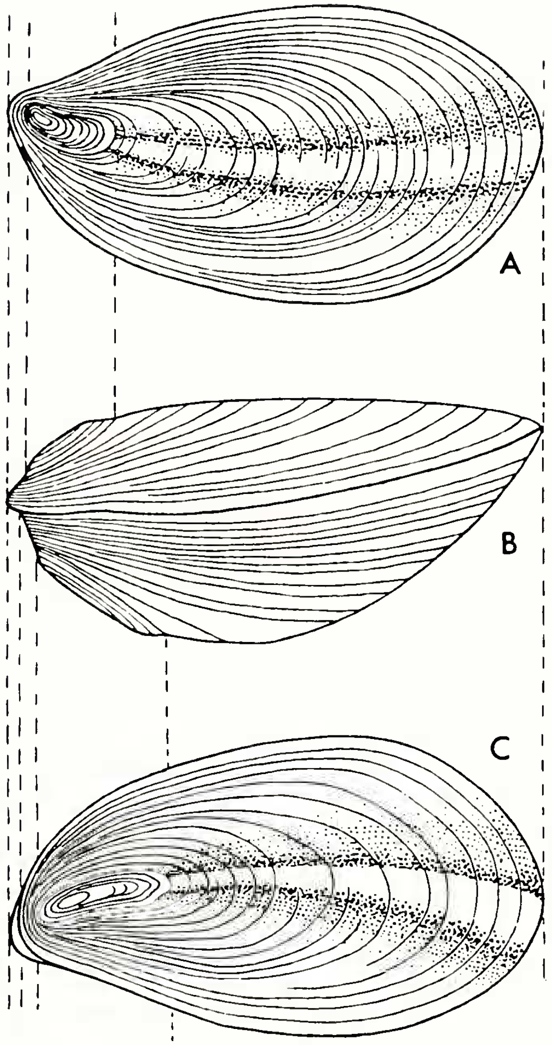

Fig. 2. Stenothecoida. A, dorsal, B, right side, C, ventral view of *Stenothecoides*. About ten times natural size. (Yochelson, 1969, fig. 3)

Although it is popular to speak of classification based on ancestor-descendent relationships, there is no way to determine these relationships apart from which comes first in the fossil record. An additional complication is that evolution need not proceed in a straight line. If one wanted to concentrate on diversity, an alternative could be to define

Mollusca as univalves. That done, a phylum Bivalvia might be proposed, with Stenothecoidea and Pelecypoda as classes within it. Bivalved gastropods are a complication, but one might make them another class of Bivalvia. At the least, this might stir debate on whether a classification based on hard part morphology of fossils should be subservient to one based on soft parts of living forms. Were such a phylum accepted, *Fordilla* could well form another class. My objections to its strange internal markings and my suggested reconstruction of soft parts different from typical Bivalvia has had no impact whatsoever (Yochelson, 1981)

"There is a significant stratigraphic gap in the fossil record of the pelecypods, between the occurrence of *Fordilla* in the late Early Cambrian and the Early Ordovician (Tremadocian-Arenigian) when the pelecypods undergo a major radiation" (Pojeta, 1975:371). Time gaps in the fossil record are to be expected where one is dealing with rare forms, but long gaps where the forms are widespread and abundant below and above a gap ought to suggest something is not quite right. In reporting a presumed pelecypod slightly older than *Fordilla*, Jell (1980:239) noted "Yochelson's other argument – the stratigraphic gap in the fossil record of pelecypods in Middle and Upper Cambrian – may disappear in the future as more finds are made." The gap is still there.

I do not really think that all bivalved mollusks will be placed in a separate phylum, but I mention this to show again that classification may be approached from different viewpoints. In turn that affects what is and what is not accepted as a class.

CLASS HYOLITHA

The hyoliths (Fig. 3) have been variously ancient "pteropods" (see Yochelson, 1979), a class of Mollusca (Marek and Yochelson, 1976), or a separate phylum (Runnegar *et al.*, 1975a). These fossils are abundant in some places in the Cambrian, but taper off rapidly in younger strata and die out by the end of the Paleozoic.

The most common hyolith order is the Hyolithida, bilaterally symmetrical closed tubes, uniformly expanding and generally with a triangular cross-section. The lower part of the aperture extends forward as a rounded shelf and the aperture is closed by an operculum; some opercula suggest a tooth and socket arrangement with the shell. Between the operculum and apertural margin are a pair of flattened curved pieces of calcium carbonate (= helens).

The Orthothecida are generally smaller, have a cross-section that may be circular, oval, or kidney bean-shaped among other configurations. The aperture lacks an anterior shelf. The operculum is simpler than that of the

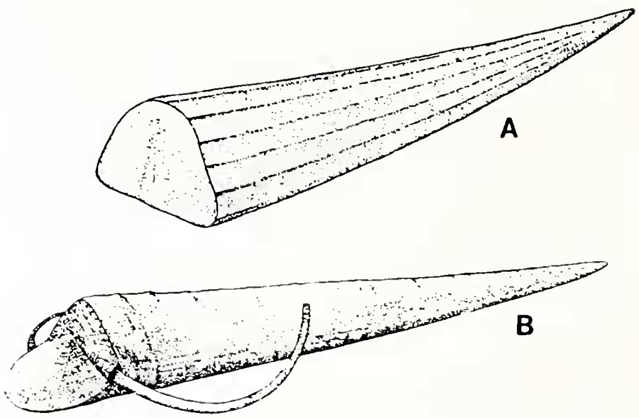

Fig. 3. Hyolitha. A. Reconstruction of *Orthotheca*. Slightly enlarged from natural size (Marek, 1963, fig. 13). B. Reconstruction of *Hyolithes*. Slightly reduced from natural size (Marek, 1963, fig. 12).

Hyolithida and does not show internal processes that would indicate hingement to the shell dorsum.

The Class Xenoconchia Shimanskiy (1963) contained Mississippian and Permian forms found in the Soviet Union. The older forms may have been platyceratid gastropods, which clung to crinoid calyxes and developed a variety of shapes, including nearly symmetrical cones. Some Permian fossils from Greenland may have been the largest Paleozoic fossil invertebrates, apart from giant cephalopods (Peel and Yochelson, 1981). In our judgement, these Permian xenoconchids were better placed as a third order within the Class Hyolitha (Peel and Yochelson, 1984). So far as I know the name Xenoconchia has not since appeared in the literature, except one suggestion that they are internal shells of cephalopods, an unlikely interpretation. These fossils have not entered into discussions on the class/phylum rank for the hyoliths.

The reconstruction of Runnegar *et al.* (1975) shows the closely folded gut of an orthothecid within the shell of a hyolithid. The peculiar "helens" projecting between operculum and apertural margin are fascinating, but they are an ordinal feature, neither a class characteristic nor a phylum characteristic. Others have objected to that reconstruction (Marek *et al.*, 1997).

However, "... it depends on one's concept of the phylum Mollusca. If one believes that all molluscs are descended from forms that had developed a dorsal exoskeleton, it is possible to exclude the Hyolitha from the phylum. The known muscle insertions of hyoliths suggest that their skeleton was not primitively dorsal" (Runnegar, 1978:332). Runnegar (1980) again discussed his concept of a phylum Hyolitha and, once they were removed from the Mollusca, they were not again discussed with that phylum

(Runnegar, 1983). Since the Monoplacophora are judged by Runnegar and others to be the stem group from which all other Mollusca are derived, the Hyolitha cannot be Mollusca. Possibly the only objective way to form an opinion of this highly subjective matter is for an interested person to read the paper by Runneger *et al.* (1975) coordinate with that of Marek and Yochelson (1976). Hyolitha are distinct from Gastropoda, or Rostroconchia, but I do not see that they are so vastly different as to be a separate phylum.

A tangential point is a recent redefinition of Monoplacophora in which that class term is abandoned for Tergomya (Peel, 1991). These forms, "classical" monoplacophorans if you will, begin in the Late Cambrian, not the Early Cambrian. Other small curved forms were placed in the extinct class Helcionelloida (Peel, 1991; Gubanov, 2000). It is too soon to claim that Helcionelloida has found acceptance as a molluscan extinct class, but its prospects are promising.

WHAT IS A PALEOZOIC MOLLUSK?

My involvement with Hyolitha brought the issue of how one defines a mollusk without considering soft parts. "Pragmatically defined a fossil mollusk is an organism whose hard parts show most of the following items: 1. The shell is composed predominately of calcium carbonate and may contain both calcite and aragonite; 2. The shell is layered and not pierced by holes; 3. The shell shows prominent growth lines; 4. The shell shows a logarithmic growth pattern; 5. The shell is basically a univalve, but may be modified to a bivalved condition; 6. The shell has basic bilateral symmetry, but may be modified to an asymmetrical condition; 7. The shell shows no trace of an apical attachment disk or foramen; 8. The shell may contain septa, either longitudinal or transverse; 9. The shell may have an operculum associated with it" (Yochelson, 1963:163).

That 1963 paper discussed the Class Coniconchia Liashenko, and I suggested two unrelated groups were involved, *Tentaculites* in a broad sense and *Hyolithes* in a broad sense. My objection was that Coniconchia seemed to have too wide a span of morphology, even though both forms were elongate tubes closed at the apex. Before anyone notes that I suggested both *Hyolithes* and *Tentaculites* might be mollusks, this was more than three decades ago and I knew even less than I know now. I have recanted on the latter. A considerable body of literature exists on both large and small tentaculitids. The small ones show more details of form and ornament than was anticipated half a century ago; possibly they were pelagic. Many of the large tubes are judged to have lived point down in sediment and presumably lived by filter feeding.

An elaborate systematic scheme has been developed for the Class Tentaculita (Farsan, 1994) which has been assigned to the Mollusca. My opinion is that including these fossils stretches the phylum beyond reasonable limits. They do not seem to have one of the basic features of Mollusca. The tube-like shell contains a multiple number of very thin layers; it is laminated. The Tentaculita are unique at the highest level and an extinct phylum is appropriate.

In a critique, "I proposed a list of features considered common to all or most molluscs (Yochelson 1961) [sic] in an attempt to define that phylum without reference to soft parts; there has been no discussion of this approach, nor of the features listed. The late Cambrian molluscan class Mattheva has no relationship to the various asymmetrical phosphatic sclerites discussed by Matthews and Missarzhevsky (1975:298-299): the latter separate these on morphological rather than chemical grounds. It does not follow, however, that all fossils with hard parts of calcium carbonate are molluscs, and there is no consensus among workers as to what fossils should be included in the phylum or excluded from it. Thus, Runnegar *et al.* (1975) suggest that *Hyolithes* and its allies constitute an extinct phylum, whereas Marek and Yochelson (1976) continue to place them as an extinct class of Mollusca" (Yochelson, 1975). There still has been essentially no more discussion of characterizing Mollusca from only the hard parts.

It is not easy to define a mollusk, living or dead. "Because no single soft- or hard part character or combination of a relatively few characters, is common to all mollusks, it is not possible to frame a succinct morphological definition of the phylum Mollusca as can be done for such phyla as the Echinodermata and Chordata. ... Mollusks are unified by morphological gradations between the different forms, by embryological similarities, and by information deduced from fossils of the various classes assigned to the phylum" (Pojeta, 1980:55).

It seems to me that possession of the mineral aragonite is basic to Mollusca and could be the reason that many fossils are not well preserved; reversion of the original shell to calcite may explain why most shells preserved in limestone exfoliate and leave only the internal mold. Immediately following in importance to shell mineralogy, I would list shell structure. A "thought experiment" is to imagine that the scaphopods are all extinct and wonder how they would be classified. Probably they would be considered "worm tubes" until someone making thin-sections saw a similarity to the shell structure of gastropods.

Similarly, one could imagine that Cephalopoda were known only from the living octopus in today's seas. Where would paleontologists place all the straight, curved and coiled septate fossil shells. If they were satisfied by shell composition, and microstructure that these were mollusks, surely the fossils would have to be assigned to a class, all of whose members were extinct. Debate between malacologists and paleontologists could break down as each group looks at different features for high-level classification within the Mollusca.

Worm tubes can produce an amazing variety of shapes and it might be educational and enlightening to compare the presumed Ordovician and Silurian larval gastropods of Dzik (1994) with a Middle Ordovician population of highly variable worm tubes (Bockelie and Yochelson, 1979). Every author, including the present one, is selective in citation of references. For an excellent example of this process, Dzik illustrated *Januspira* as a monoplacophoran, following Runnegar (1977), whereas an interpretation on the following page (Yochelson, 1977) of it as a bizarre worm tube was ignored.

In the past, a number of strange fossils were tossed into the Mollusca. A Paleozoic scaphopod may be a worm tube (Yochelson and Goodison, 1999) or a monoplacophoran may be a medusoid (Webers and Yochelson, 1999); it depends on what features one considers to be most significant. To begin to make sense of the Mollusca, one should remove those fossils that ought not to be in the phylum. Unfortunately, by some workers ignoring composition of the integument, or great variation in shape, or concentrating on internal molds, there is danger of further confusing the fossil record of the Mollusca.

EVOLUTION

Patterns in evolution is another subject with much discussion and little resolution. One notion that may have wide acceptance is that of adaptive radiation - a new form appears and diversifies rapidly, at least rapidly on the geologic time scale. The concept was first clearly enunciated in regard to early Cenozoic land mammals, but it seems to apply to other organisms, plant and animal, at other times and at various taxonomic levels. There is a near consensus that the early record of both Arthropoda and Echinodermata includes much high-level differentiation; in the Echinodermata, the number of extinct classes could be double those that are extant (Campbell and Marshall, 1987).

If adaptive radiation is a general phenomenon, why does the phylum Mollusca have a different pattern? In one evolutionary scheme (Runnegar and Pojeta, 1974; Pojeta and Runnegar, 1976) there is room for only one extinct class. "At least six [of the eight] higher taxa of Mollusca originated in the Early Cambrian and did not begin to radiate in any substantial way until the late Cambrian or early Ordovician" (Runnegar, 1987:50). In this scheme, the Cephalopoda is the only class that appears in the Late Cambrian and immediately undergoes radiation. Scaphopoda appeared even later in the fossil record.

In an alternative interpretation (Yochelson, 1978) most Cambrian mollusks superficially resemble those in extant classes, but are actually products of an early adaptive radiation; the extant classes come later. It is impossible to demonstrate that one of these two approaches is true and one is false, but I would be less than human if I did not prefer my view. With the latter approach one will seek and find fossils that belong to extinct classes, and with the former, one will not. Fossils do not have their systematic position inscribed on the shell and there is room for honest disagreement when unusual or poorly preserved material is at hand. Despite what has been written (Runnegar and Pojeta, 1974), there is no single paleontological viewpoint.

I am not qualified to discuss the mechanism of evolution of classes. In 1978, I guessed at a non-shelled form beginning in the Precambrian and existing to at least mid-Paleozoic as the source for the various classes, but now think it was a bad guess. Changes that are recognized as being of class rank could have developed in the larval stage. I do not necessarily think that major steps happened instantly, but with the current resolution in stratigraphy, they appear to be instantaneous.

The similarity of shell throughout the Mollusca may suggest that an organic template formed originally and then the mollusks diversified. The mechanism of formation of hard parts in the Phanerozoic is still a murky area. It can be made murkier, for did the hypothetical noncalcified mollusk form a calcified hard part or parts, or did having a platform on which to anchor musculature result in a fundamentally different organism? Put more starkly, did the mollusk make a shell or did the shell make the mollusk?

SUMMARY

"The poor Middle and Late Cambrian record of the Gastropoda, Pelecypoda and Rostroconchia . . . is difficult to explain. Possibly more fossils of these groups will be found when more microfossils are extracted from Cambrian rocks" (Runnegar, 1978:333). We are still waiting. If gaps in the record are real, there may be merit in considering that the later record of the mollusks consists of convergent forms rather than direct ancestors.

As mentioned, a fundamental problem is what fossils should be placed in the Mollusca. A second problem is what is the level of distinctiveness that makes one fossil a representative of an extant class and another a representative of an extinct one. Even if those points are resolved, others may be irreconcilable. In his view, Runnegar (1983) refuted my refutation of the Runnegar and Pojeta hypothesis. This "yes it is and no it is not" has hardened both positions. If one side were to concede that hyoliths were not mollusks, would the other concede that the rostroconchs are simply peculiar pelecypods? In the long run, science might not be better served, but we could save a lot of time and paper if we agree that there are no extinct classes of mollusks.

For some specialists, "Higher taxa are recognized largely by hindsight, after sufficient evolution and diversification have produced a cohesive group of related organisms" (Runnegar, 1978:329). Likewise "If this symposium had been held in the Early Cambrian, it is probable that *Fordilla* and *Pojetia* would, at best, be ranked as a family or superfamily of the Monoplacophora" (Runnegar, 1987:49).

It is a cheap shot to note the clarity of 20/20 hindsight vision. In investigations of classification, should emphasis be on the product – morphology of the organism itself – or on the process – interpretation of ancestor-descendent relationships? My position is that one classifies on the basis of the features that are preserved. I admit this is very much an old-fashioned viewpoint.

LITERATURE CITED

Bockelie, Tove and E. L. Yochelson. 1979. Variation in a species of "worm" from the Ordovician of Spitsbergen. *Norsk Polarinstitutt Skrifter* 167:225-237.

Dzik, Jerzy. 1994. Evolution of 'small shelly fossils' assemblages. *Acta Palaeontologica Polonica* 39:247-313.

Campbell, K. W. S. and C. R. Marshall. 1987. Rates of evolution among Paleozoic echinoderms. *In: Rates of Evolution*, K. W. S. Campbell and M. F. Day, eds. pp. 61-100. Allen and Unwin, London.

Farsan, N. M. 1994. Tentaculiten: Ontogenese, Systematik, Phylogenese, Biostratonomie und Morphologie. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 547:1-128.

Gould, S. J. 1989. *Wonderful Life*. W. W. Norton, Inc. New York.

Gubanov, A. P. 2000. *Evolution of the earliest molluscs*. Department of Earth Sciences-Historical geology and paleontology, Uppsala University. 28 pp. + 14 included papers.

Jell, P. A. 1980. Earliest known pelecypod on Earth - a new Early Cambrian genus from South Australia. *Alcheringa* 4:233-239.

Marek, L. 1963. New knowledge on the morphology of Hyolithes. *Sbornick Geologickych* Ved. *Paleontologie*, Prada P, sv 1: 53-73.

Marek, L., R. L. Parsley, and A. Gallé. 1997. Functional morphology of hyoliths based on flume studies. *Vestnik Ceskeho geologickeho ustavu* 72:351-358.

Marek, L. and E. L. Yochelson. 1976. Aspects of the biology of Hyolitha. *Lethaia* 9:65-82.

Matthews, S. C. and V. V. Missarzhevsky. 1975. Small shelly fossils of late Precambrian and early Cambrian age: a review of recent work. *Journal of the Geological Society of London* 131:289-304.

Peel, J. S. 1991. The classes Tergomya and Helcionelloida, and early molluscan evolution. *Grønlands Geologiske Undersøgelse Bulletin* 161:11-65.

Peel, J. S. and E. L. Yochelson. 1981. Giant Mollusca (Hyolitha) from the Permian of East Greenland. *Rapport Grønlands Geologiske Undersøgelse Bulletin* 101:65-67.

Peel, J. S. and E. L. Yochelson. 1984. Permian Toxeumorphida from Greenland: an appraisal of the molluscan class Xenoconchia. *Lethaia* 17:211-221.

Pojeta, J., Jr. 1975. *Fordilla troyensis* Barrande and early pelecypod phylogeny. *Bulletins of American Paleontology* 67:363-384.

Pojeta, J., Jr. 1980. Molluscan phylogeny. *Tulane Studies in Geology and Paleontology* 16:55-80.

Pojeta, J., Jr. and B. Runnegar. 1974. *Fordilla troyensis* and the early history of pelecypod mollusks. *American Scientist* 62:706-711.

Pojeta, J., Jr. and B. Runnegar. 1976. The paleontology of rostroconch mollusks and the early history of the Phylum Mollusca. *U. S. Geological Survey Professional Paper* 968.

Pojeta, J., Jr., B. Runnegar, and J. Kříž. 1973. *Fordilla troyensis* Barrande: the oldest known pelecypod. *Science* 180:866-868.

Pojeta, J., Jr., B. Runnegar, N. J. Morris, and N. D. Newell. 1972. Rostroconchia: a new class of bivalved mollusks. *Science* 177:264-267.

Regan, C. T. 1925. Organic evolution [address by sectional president]. *British Association for the Advancement of Science*, Southampton, Section D:D1-D12.

Runnegar, B. 1977. Found – a phylum for *Januspira*. *Lethaia* 10:203.

Runnegar, B. 1978. Origin and evolution of the Class Rostroconchia. *Philosophical Transactions of the Royal Society of London series B* 284:319-333.

Runnegar, B. 1980. Hyolitha: status of the phylum. *Lethaia* 13:21-25.

Runnegar, B. 1983. Molluscan phylogeny revisited. *Association of Australian Palaeontologists Memoir* 1:121-144.

Runnegar, B. 1987. Rates and modes of evolution in the Mollusca. *In: Rates of Evolution*, K. S. W. Campbell and M. F. Day, eds. pp. 39-60. Allen and Unwin, London.

Runnegar, B. and J. Pojeta, Jr. 1974. Molluscan phylogeny: the paleontological viewpoint. *Science* 186:311-317.

Runnegar, B., J. Pojeta, Jr., N. J. Morris, J. D. Taylor, M. E. Taylor, and G. McClung. 1975. Biology of Hyolitha. *Lethaia* 8:181-191.

Runnegar, B., J. Pojeta, Jr., M. E. Taylor, and D. Collins. 1979. New species of Cambrian and Ordovician chitons *Matthevia* and *Chelodes* from Wisconsin and Queensland: evidence for the early history of polyplacophoran mollusks. *Journal of Paleontology* 53:374-394.

Shimanskiy, V. N. 1963. [Systematic position and scope of Xenoconchia] *Paleontologiske Zhurnal* (4):53-63. [Translated by American Geological Institute].

Waller, T. R. 1998. Origin of the molluscan Class Bivalvia and a phylogeny of major groups. *In: Bivalves: an eon of evolution*, P. A. Johnston and J. W. Haggart, eds. pp. 1-45. University of Calgary Press.

Webers, G. F. and Yochelson, E. L. 1999. A revision of *Palaeacmaea* (Upper Cambrian) (?Cnidaria). *Journal of Paleontology* 73:598-607.

Yochelson, E. L. 1963. Notes on the class Coniconchia. *Journal of Paleontology* 35:162-167.

Yochelson, E. L. 1966. Mattheva, a proposed new class of mollusks. *U. S. Geological Survey Professional Paper* 523:B1-B13.

Yochelson, E. L. 1968. Stenothecoida, a proposed new class of Cambrian Mollusca. *International Palaeontological Union*, Prague, Abstracts, p. 34.

Yochelson, E. L. 1969. Stenothecoida, a proposed new class of Cambrian Mollusca. *Lethaia* 2:49-62.

Yochelson, E. L. 1975. Discussion of early Cambrian "molluscs." *Journal of the Geological Society of London* 131(6):661-662.

Yochelson, E. L. 1977. Comments on *Januspira*. *Lethaia* 10:204

Yochelson, E. L. 1978. An alternative approach to the interpretation of the phylogeny of ancient mollusks. *Malacologia* 17(2):185-191.

Yochelson, E. L. 1979. Early radiation of Mollusca and Mollusc-like groups. *In: The Origin of Major Invertebrate Groups*, M. R. House, ed. pp. 157-178. Systematics Association, special volume

12. Academic Press, London, Oxford University Press, Oxford, England.

Yochelson, E. L. 1981. *Fordilla troyensis* Barrande: "The oldest known pelecypod" may not be a pelecypod. *Journal of Paleontology* 55:113-125.

Yochelson, E. L. 1984. Speculative functional morphology and morphology that could not function: The example of *Hyolithes* and *Biconulites*. *Malacologia* 25(1):255-264.

Yochelson, E. L. and R. Goodison, R. 1999. Devonian *Dentalium martini* Whitfield, 1882, is not a mollusk but a worm. *Journal of Paleontology* 73:634-641.

Yu Wen. 1984. Early Cambrian molluscan faunas of Meischucan Stage, with special reference to Precambrian-Cambrian Boundary. *In: Contributions to the 27th International Geological Congress*, Sun Shu, ed. pp. 21-25.

Yu Wen. 1990. The first radiation of the shelled molluscs. *Palaeontologia Cathayana* 5:139-170.

Yu Wen. 1996. Early Cambrian stenothecoid molluscs from China. *Records of the Western Australian Museum* 18:209-217.

Date of manuscript acceptance: 23 June 2000